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Species-specific weather response in the daily stem variation cycles of Mediterranean pine-oak mixed stands

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ABSTRACT

Climate change forecasts are particularly severe for the western Mediterranean Basin, where rising temperatures and decreased precipitation could increase the frequency of drought events. Understanding the specific weather drivers of radial variation in Mediterranean mixed forest stands will allow us to better predict the ecological and production alterations that may result from climate change. Here, we studied species differences in stem daily radial variation cycles and daily radial increment of Mediterranean pine-oak (*Pinus pinaster-Quercus pyrenaica*) mixed stands over three climatically contrasted years (2012-2014) at two sites with dissimilar drought conditions. Our aim was to uncover differences in the weather drivers of daily radial variation for the two co-existing species. High-resolution point dendrometers were installed in dominant oak and pine trees, so that daily radial variation cycles were analyzed. Linear mixed models were fitted to analyze species-specific response to weather. Air temperature leads to radial stem-size changes in daily variation cycles with different species responses. Precipitation increased daily radial variation and cycle duration in the same way for both species. Daily radial increment and number of cycles with increment phase during spring was mostly higher for pine than oak, and water availability was the most important control factor for the phase mentioned. Differences in species response to weather conditions may offset the usual low production of pure oak coppice Mediterranean stands and highlight the role of mixed forests as a possible adaptation strategy for climate change.

1. Introduction

Climate change may impact Mediterranean forests harshly (Dankers and Hiederer, 2008). Changes in extreme climatic conditions, such as more frequent and severe summer droughts, might affect the provision of goods and forest services (Hanewinkel et al., 2012). Climate change could influence biodiversity and ecosystem functioning through phenological alterations (Gordo and Sanz, 2009; Rossi et al., 2011), species-specific distribution range shifts (Peñuelas et al., 2007), changes in forest production (Linares and Camarero, 2012; Pretzsch et al., 2014) and subsequent changes in carbon storage (Vayreda et al., 2012).

Projected climate changes give urgency to the need for a better understanding of the effects of meteorological factors on growth in Mediterranean forests. Rising temperatures and drought events seem to be the key causes of tree decline in Mediterranean forests, despite tree acclimation to cope with climate change through phenological changes and increased water-use efficiency (Hartmann et al., 2015; Natalini et al., 2016; Peñuelas et al., 2011).

In this context, mixed forest stands could play an important role in preventing or reducing adverse changes. Mixed species stands might be more stable than monospecific ones, because of their greater resilience and resistance to biotic and abiotic factors (Guyot et al., 2016; Knoke et al., 2008; Pretzsch et al., 2013) and their higher temporal stability (Jucker et al., 2014; del Río et al., 2017). Mixtures could increase resistance and resilience in extreme drought conditions through complementary use of water resources based on species niche partitioning and alterations in water-use efficiency (Forrester, 2014). Although studies have shown contrasting results depending on species composition and site conditions, the positive effect of mixing species seems relevant to drought-prone sites (Grossiord et al., 2014; Forrester et al., 2016).

Monitoring stem radial variations can provide insight into intra-annual stem dynamics and improve our understanding of climate impacts on tree physiology and growth processes (Deslauriers et al., 2007; Duchesne and Houle, 2011; Zweifel, 2016). Continuous or high-resolution dendrometer recordings provide valuable information on tree stem radial variation along with the possibility of studying tree response to environmental influences at a high temporal resolution (Siegmund et al., 2016). High-resolution dendrometers are commonly used for studying seasonal tree growth dynamics, uncovering the environmental parameters that drive tree growth, and monitoring aspects of tree water balance such as water use and drought stress (Van der Maaten et al., 2016; Zweifel, 2016; Zweifel et al., 2016). Consequently, automatic dendrometers are now widely used to provide high-resolution stem variation data on coniferous and broadleaf trees from boreal to tropical forests (Biondi and Rossi, 2015; Deslauriers et al., 2007; Duchesne and Houle, 2011). However, because these analyses often involve short observation periods, they do not accurately capture radial variations under contrasting weather conditions (Drew and Downes, 2009; King et al., 2013).

The handful of studies that have reported on seasonal variations in tree stem radius in Mediterranean areas mostly confirm the dominant role of temperature as the major constraint on radial increment in short time scales, and of precipitation effects in monthly scales (Camarero et al., 2010; Gutiérrez et al., 2011; Vieira et al., 2013). High-resolution stem diameter variation studies on mixed forests in this region are also infrequent. Sánchez-Costa et al., (2015) found contrasting growth and water use strategies in four co-occurring Mediterranean species, and Camarero et al., (2010) reported species-specific differences in xylogenesis patterns in mixed stands of *Juniperus thurifera* L., *Pinus halepensis* Mill., and *Pinus sylvestris* L. However, very little research is available concerning daily radial variation cycles in mixed stands, so remains unclear in the Mediterranean climate.

Recent studies have shown that the Mediterranean tree species *Pinus pinaster* Ait. and *Quercus pyrenaica* Willd are highly vulnerable to intense drought events (Gea-Izquierdo et al., 2013; Prieto-Recio et al., 2015). *P.pinaster* is one of the most common pine tree species in Spain and usually establishes spontaneous mixed stands with *Q.pyrenaica*. Consequently, forest management strategies during the second half of the twentieth century included re-introducing pine into oak coppice stands. These co-occurring species show different successional and phenological traits: light-demanding pine species are dominant in early successional stages, while deciduous oak is a moderately shade-tolerant tree that predominates in the late-successional stage. Studies of radial variation cycles focusing on these species are insufficient, with the exception of Vieira et al. (2013), who worked with *P.pinaster* for one year only (2010). A previous study by Aldea et al. (2017) on the same stands used in the current work, showed species differences in radial increment patterns and positive effects from heavy thinning.

For the research presented here, we used high-resolution dendrometer data to investigate species-specific tree responses to contrasted meteorological conditions in Mediterranean pine-oak mixed forest stands during the 2012–2014 period. The aims of the present study were 1) to show species differences in daily radial variation cycles, 2) to uncover species-specific weather responses in daily radial variation cycles and 3) to identify the weather variables that drove radial increment. We tested the hypotheses that (i) daily radial variation cycles varied according to seasons and species; (ii) differences were due to species responding differently to weather conditions and (iii) temperature and water availability were the main factors limiting radial increment, as expected in Mediterranean areas.

2. Materials and methods

2.1. Study sites

The study took place at two experimental sites with different drought conditions in central Spain: Lubia (Soria; 41° 39′ N, 2° 29′ W) and San Pablo de los Montes (Toledo; 39° 31′ N, 4° 16.6′W). The Lubia site was located at an altitude of 1134 m.a.s.l. on a continental plateau. It has a sub-humid continental Mediterranean climate with an annual rainfall of 512 ± 133 mm, of which 100 ± 49 mm falls during the summer drought period, between June and August (AEMET, 2016; Spanish State Meteorological Agency). Annual mean temperature is 10.0 ± 1.6 °C and the hottest month is July, with an average temperature of 18.9 ± 2.9 °C. Frost occurs from September to May.

The site at San Pablo de los Montes was established in the Montes de Toledo mountain range at 1,102 m.a.s.l. It has a continental Mediterranean climate, average rainfall of 469 ± 122 mm and a marked summer drought between June and August, with 49 ± 51 mm recorded rainfall (AEMET, 2016). Annual mean temperature is 12.9 ± 0.6 °C and the hottest month is July, with an average temperature of 23.9 ± 1.1 °C. Frost occurs from November to March.

The Walter-Lieth annual aridity index (WAI), defined as the quotient between the dry and wet season areas from climograms based on historical climate records (1981-2010; AEMET, 2016), was calculated using 'BIOdry' R package (Lara et al., 2013). The WAI index revealed drought differences between sites: WAI of 0.22 for Lubia and 0.65 for San Pablo de los Montes. Hereafter, we will refer to these sites as WAI-0.22 and WAI-0.65, respectively.The forest stands at both sites have similar origins: The initial oak coppice stands were completely harvested by clear-cutting during the 1970s, followed by afforestation with pines sown in rows. Oak coppice sprouts grew between the pine rows, and today the stand looks like a pine-oak even-aged mixed stand, though real cambial age differs between species

2.2. Stem radial variation and climatic measurements

Three dominant trees per species and site (twelve trees in total) were selected for installation of electronic point dendrometers. The pine trees chosen for sampling were 268.8 mm (standard deviation (sd) of 15.3 mm) in diameter at breast height and 11.2 m (0.7 m sd) high, while the oaks were 94.5 mm (7.3 mm sd) in diameter and 7.4 m (0.8 m sd) high. Besides, there were no significant differences in species diameter, height or age (for pine) between sites.

In autumn 2011, we installed electronic point dendrometers (Depfor, University of Huelva, details are available in Vázquez-Piqué et al., 2009) with a resolution of 1 μm in the selected trees to measure stem radial variation at breast height. The dead outermost layers of bark were carefully removed to avoid cambium damage and to eliminate hygroscopic influences from bark (shrinking and swelling due to change in air humidity) on dendrometer measurements. Data loggers were programmed to record measurements every 15 min for the entire 2012–2014 study period.

Site weather variables were continuously monitored using a variety of sensors. Air temperature, relative humidity and dew point were recorded at 15 min resolution using a data logger (HOBO U12 4-External Channel) placed at the WAI-0.22 site. A weather station (HOBO) was installed at the WAI-0.65 site to record air temperature, relative humidity, rainfall, solar radiation and wind speed. Additionally, temperature, precipitation and radiation records were compiled using hourly data from the AEMET automatic network stations (Lubia-Ceder 2044B and San Pablo de los Montes 3298X) located 6 km and 5 km from the WAI-0.22 and WAI-0.65 sites, respectively, to fill gaps in the climate information. Correlation between on site meteorological records and the network station was 0.978 and 0.969 for WAI-0.65 and WAI-0.22 sites, respectively. Records filled from network station data accounted for 9.2% (9.729 hourly records) and 29.6% (31.169 hourly records) of the total for WAI-0.65 and WAI-0.22, respectively. Mean vapor pressure deficit was also estimated from former weather measurements, and we applied indirect method described by Zweifel et al., (2005), to calculate tree water deficit by tree and year, using dendrometer measurements to quantify drought stress based on potential linear growth during periods
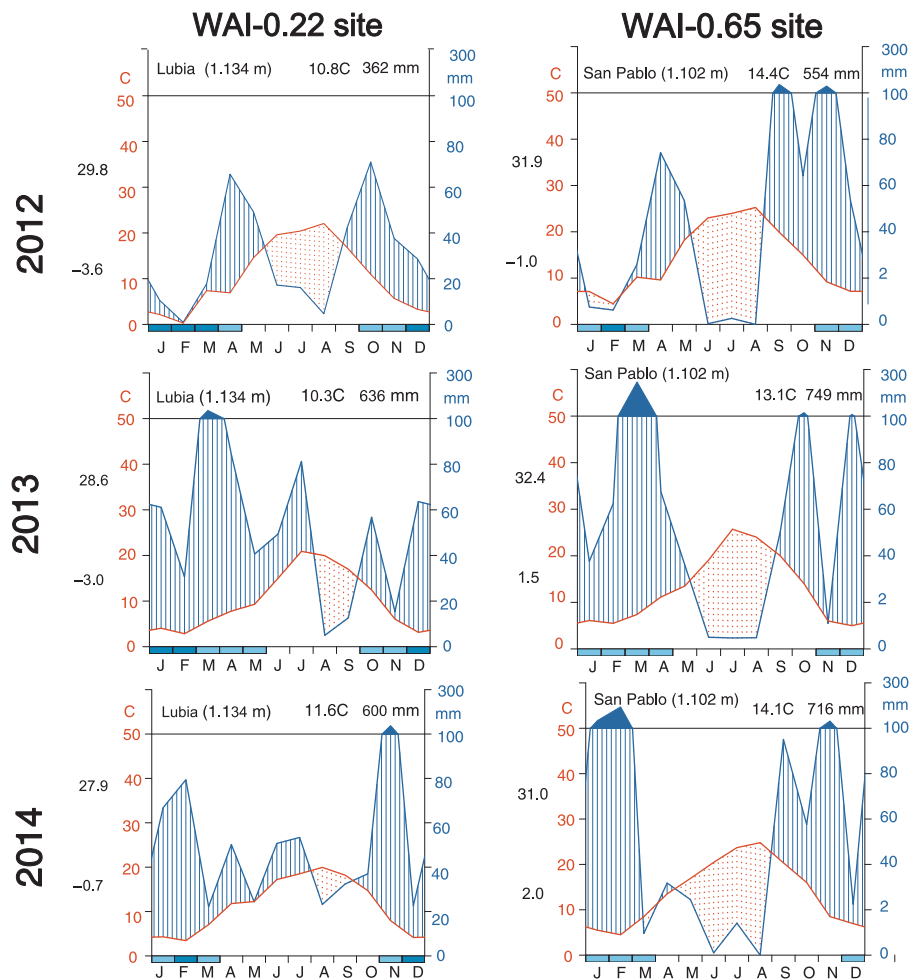
Fig. 1. Climograms of sampling years by site. Numbers to the left of y-axis indicate average daily maximum temperatures of the warmest month and average daily minimum temperatures of the coldest month, from top to bottom, respectively.

of stem shrinkage (Zweifel, 2016).

Summer drought was severe in 2012 at the WAI-0.22 site, while 2013 and 2014 had high spring and autumn rainfall, respectively (Fig. 1). Conversely, summer drought was present in all sampling years at WAI-0.65, but precipitation was very low at both sites during winter and spring of 2012.

2.3. Data analysis

2.3.1. Radial stem variation cycle approach

The sub-hourly dendrometer values were averaged to hourly resolution to link them with environmental variables, as well as to identify and correct errors or wrong measurements. Gaps of short duration (lower than a day, longer gaps remained unfilled) and abrupt jumps were corrected using an ARIMA model for the trend series from the same tree and season (Van der Maaten et al., 2016).

Daily radial variation series for each tree and year were processed individually according to the stem cycle approach (Deslauriers et al., 2011; Drew and Downes, 2009; Van der Maaten et al., 2016, 2013), which splits radial variation cycles into three different phases: (1) contraction, the period between the first maximum radius and the next minimum radius; (2) expansion, the period from the minimum to the next morning maximum; and (3) stem radial increment, part of the expansion phase from the time when the stem radius exceeds the morning maximum until the subsequent maximum (Fig. 2).

Stem radial increment (mm) and duration (hours) of the radial increment phase in the daily variation cycles were calculated for each tree

and year. We also defined several metrics based on sinusoidal waveform characteristics, in order to explore features of full daily radial variation cycles (Fig. 2). The difference between local maximum and minimum stem radius in the daily cycle is the amplitude of the cycle (mm), i.e., the maximum daily radial variation for a full cycle. Similarly, the period variable was defined as the duration, or the time (hours) required to complete a full cycle. The statistics extraction from cycle, gap filled and environmental linked was performed using 'dendrometeR' R package (Van der Maaten et al., 2016).

To better describe stem radial variation throughout the year, dendrometer series were divided into five periods or seasons according to Vieira et al. (2013): winter dormancy, during which radius variation was around zero; spring growth, from the start of positive radial increment until the spring maximum; pre-summer contraction, when the daily increment was negative; summer dormancy, when radial increment ceased and autumn, when rehydration occurred and radial increment increased rapidly in a short period of time. Radial variation cycles were defined as a symmetrical sinusoidal waveform for better visualization of daily seasonal cycles.

Species and season differences in amplitude and period for full daily cycles were calculated by applying non-parametric statistics based on global rankings, which compute simultaneous confidence intervals and adjusted p-values based on Tukey contrasts for repeated measurements. Similarly, we calculated species and year differences in magnitude (mm), duration (hours) and number of cycles with the radial increment phase using the *npar.t.test* and *mctp.rm* functions from 'nparcomp' R package (Konietschke et al., 2015).
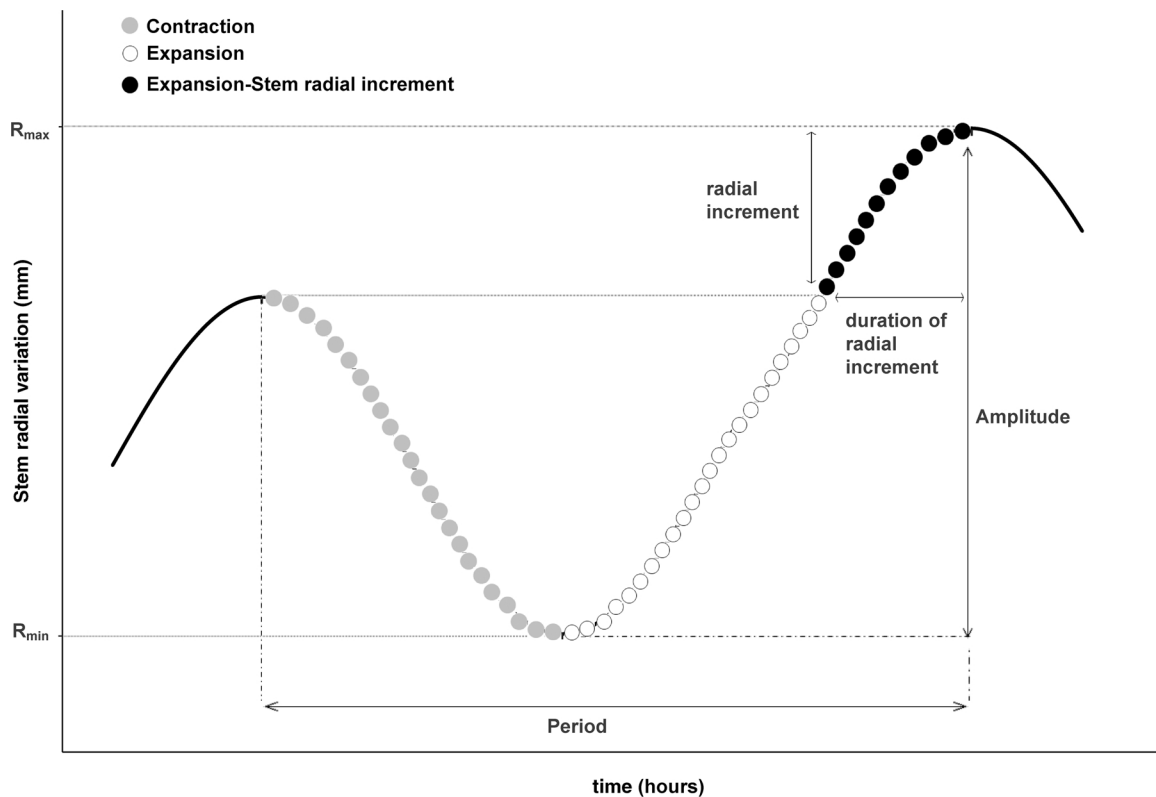
Fig. 2. Schematic representation of stem daily radial variation cycle, divided into three distinct phases: contraction (grey dots), expansion (white and black dots) and stem radial increment (black dots). Daily amplitude coincides with the magnitude of radial expansion (Rmax - Rmin). Period is the duration of full cycle.

2.3.2. Weather effect on stem radial variation cycle and increment phase

Linear mixed models were fitted to determine the influence of meteorological variables on the amplitude and period of radial variation cycles, and on the magnitude of the increment phase. To better understand the influence of meteorological variables on the increment phase, especially when growth takes place, the model was also fitted for two different time scales: annual and spring. Mean, sums (when necessary), maximum, and minimum values of meteorological variables were calculated for full cycles. The structure of the linear mixed model was as follows:

$$log(\rho_{ijk} + 1) = \alpha_0 + f(\boldsymbol{weather}) + (\alpha_1 + f(\boldsymbol{weather}))*\boldsymbol{oak} + \omega_k + u_{jk}$$

$$+ v_{ijk} + \varepsilon_{ijk} \tag{1}$$

where ρ_{ijk} is the amplitude (mm), period (hours) of full radial variation cycle or daily radial increment (mm), for tree i in site j and year k (mm); α_0 and α_1 are the intercept regression coefficients for pine and oak, respectively; $f(\boldsymbol{weather})$ is a linear function of weather variables; oak is a dummy variable with values of 1 for oak and 0 for pine; $\omega_k \sim N (0, \sigma_k)$ is the year random effect; $u_{jk} \sim N (0, \sigma_{jk})$ is the site random effect; $v_{ijk} \sim N (0, \sigma_{ijk})$ is the tree random effect and $\varepsilon_{ijk} \sim N (0, \sigma_e)$ is the error term for each individual i in each site j for year k.

Additionally, previous scatter plots were analyzed to check for possible non-linear relationships between response and weather variables. In this way, when logarithm transformation of temperature was taken into account, a value of 5 was added to the temperature variable to avoid the minimum mean hourly temperature value (above -5 °C) forcing a mathematical indeterminacy. The best random and fixed effect structures were fitted by restricted and maximum likelihood, respectively. Explanatory variables were chosen based on stepwise model selection using Akaike information criterion (AIC) to find the most parsimonious model. Multicollinearity of environmental variables was controlled by variance inflation factor values. Serial autocorrelation

was assessed by partial and autocorrelation function plots, and several serial correlation structures were evaluated (autoregressive, moving average, and a mixed autoregressive-moving average model) to account for residual autocorrelation. A variance function for modeling heteroscedasticity was used for several structures (exponential, power, and constant plus power of the absolute value of the variance covariate) (Pinheiro and Bates, 2000).

3. Results

Cumulative intra-annual radial increment patterns differed between species and among years (Fig. 3). Pine species always presented a higher spring and autumn asymptotic parameter than oak, along with a greater spring increment rate.

3.1. Seasonal differences in stem radial variation cycles

Comparisons of mean full cycles throughout the year reveal variation among seasons and species (Figs. 4 and 5). The lowest amplitudes were observed in winter, regardless of species (P < 0.01). Oak had the highest amplitude during pre-summer and summer, while amplitude was greatest for pine in spring, when growth occurs (P < 0.01 for both cases). Amplitude was higher for pine than oak during winter and spring, but the opposite occurred in pre-summer and summer (P < 0.01). However, period was always lower for pine than oak (P < 0.01), except in pre-summer and summer, when there were no differences between species (P = 0.65). The cycle period was higher during winter and autumn, and lower in summer (P < 0.05).

3.2. Weather effect on amplitude and period of stem radial variation cycles

Models fitted for weather drivers of amplitude and period showed the importance of air temperature and rain (Table 1 and Fig. 6). Water
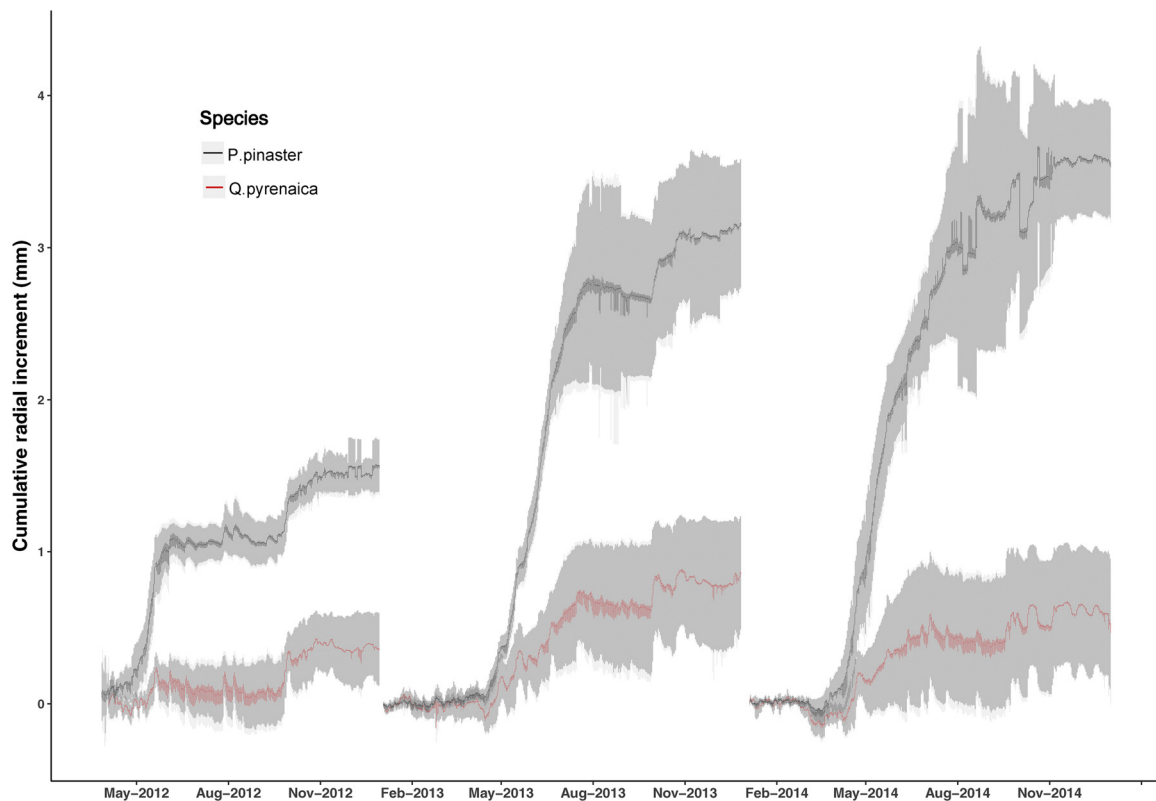
Fig. 3. Intra-annual cumulative radial increment patterns. For each species, the line represents the mean radial increment of six monitored trees, and the grey shadowed area indicates the 95% confidence intervals.

deficit was also related to high radial cycle amplitude, which supports summer observations. The effect of air temperature on the amplitude of daily cycles differed between species. In both species, amplitude increased with increasing air temperature (from 6 °C for oak), though pine presented a more moderate trend (Fig. 6). Amplitude also increased in oak species at air temperatures below 6.0 °C, according to the fitted model in Table 1. Furthermore, though period was affected by air temperature, precipitation had higher impact on both species.

3.3. Species differences in the spring radial increment phase

Daily radial increment and number of cycles with a radial increment phase varied with years and species in spring (Fig. 7). However, no differences in the duration of the increment phase between species were found (results not shown). Daily radial increment showed significant differences between species (higher for pine) during 2013 and 2014 at the WAI-0.65 site (P < 0.01, Fig. 7), and only in spring 2013 at the WAI-0.22 site (P = 0.02). The number of cycles with increment phase
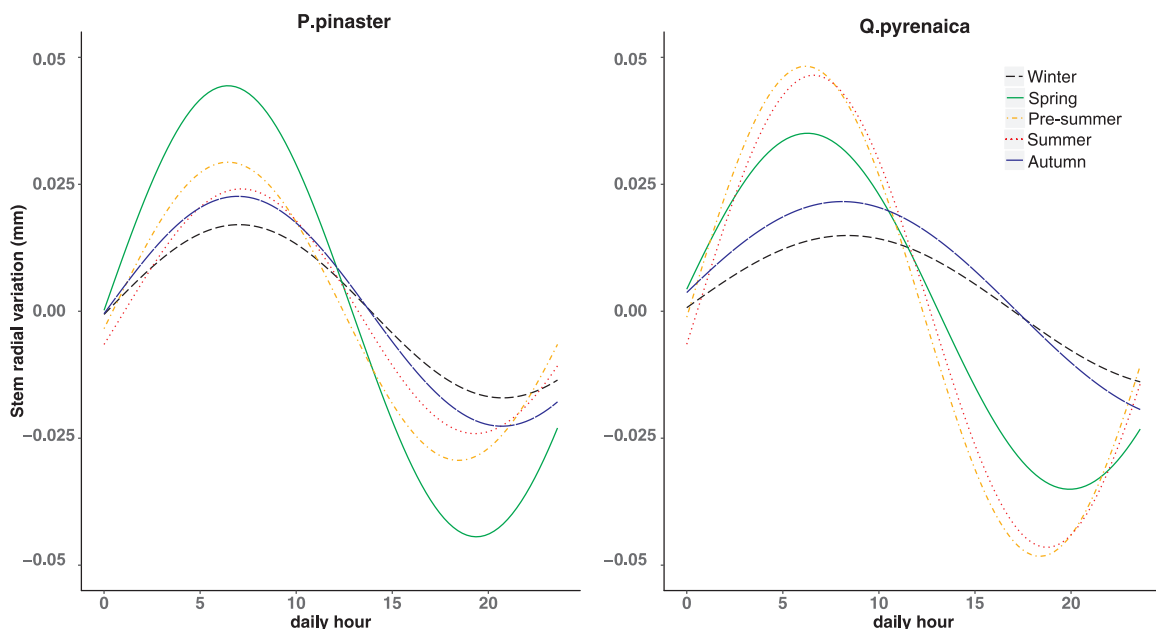

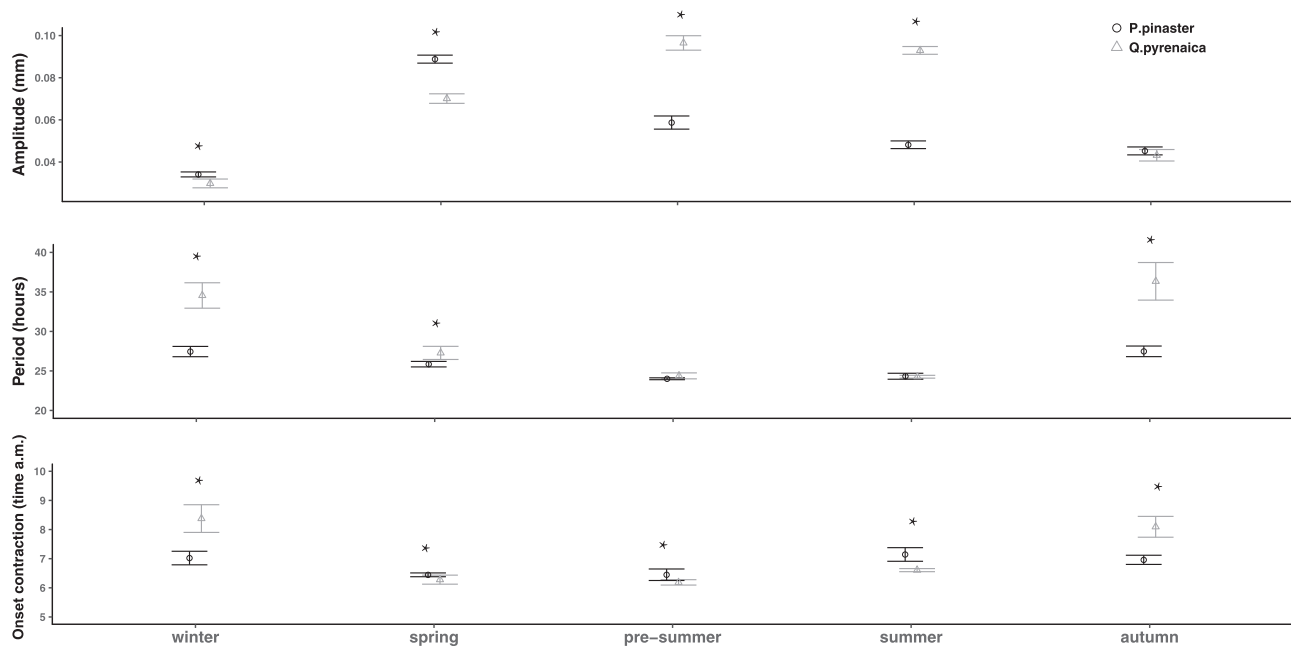**Fig. 4.** Mean daily radial variation cycles by season and species.

Fig. 5. Differences in amplitude (mm), period (hours) and onset of contraction phase for daily radial variation cycles by species and season. Error bars indicate confidence intervals (95%) and asterisk denotes significant differences between species.

Table 1

Model fitted for amplitude and period of stem radial variation cycles (Eq. (1)). Significant parameters are in bold. α_0 *and* α_1 are the intercept regression coefficients for pine and oak respectively; T_{air} is air temperature (ºC); P is daily precipitation (mm); Wd is water deficit (mm); σ_k is standard deviation for year random effect; σ_{jk} is standard deviation for site random effect; σ_{ijk} is standard deviation for tree random effect; σ_e is standard deviation for error term; φ and θ are autoregressive and moving average for ARMA(1,1) residual serial correlation parameters; δ_1 and δ_2 are function parameters used to model residual variance as an exponential function of the variance covariate vector (g_{ijk}) for amplitude: $Var(\varepsilon_{ijk}) = \sigma_e^2 \cdot e^{2\delta_1 g_{ijk}}$ or constant plus a power for period: $Var(\varepsilon_{ijk}) = \sigma_e^2(\delta_1 + |g_{ijk}|^{\delta_2})^2$.

Parameter	Amplitude		Period	
	Coefficient	p-value	Coefficient	p-value
α_0 (pine)	$1.18 \cdot 10^{-2}$	0.178	**2.995**	**< 0.001**
T_{air}(pine)	$1.63 \cdot 10^{-4}$	0.662	**−7.32·10⁻³**	**0.002**
$log(T_{air} + 5)$ (pine)	**1.05·10⁻⁴**	**0.021**	**9.94·10⁻²**	**0.005**
α_1 (oak)	**8.85·10⁻²**	**< 0.001**	$2.25 \cdot 10^{-1}$	0.066
T_{air}(oak)	**3.69·10⁻³**	**< 0.001**	$-2.41 \cdot 10^{-3}$	0.517
$log(T_{air} + 5)$ (oak)	**− 5.30·10⁻²**	**< 0.001**	$-4.98 \cdot 10^{-2}$	0.395
P	**1.52·10⁻³**	**< 0.001**	**4.34·10⁻²**	**< 0.001**
Wd	**1.70·10⁻¹**	**< 0.001**	0.081	0.098
σ_k (year)	$1.14 \cdot 10^{-6}$		$1.26 \cdot 10^{-6}$	
σ_{jk}(site)	$1.15 \cdot 10^{-6}$		$2.76 \cdot 10^{-2}$	
σ_{ijk}(tree)	$2.34 \cdot 10^{-7}$		$2.31 \cdot 10^{-2}$	
σ_e(error)	$1.62 \cdot 10^{-2}$		$2.78 \cdot 10^{-5}$	
φ	0.961		− 0.340	
θ	− 0.663		0.285	
δ_1	11.151		$2.06 \cdot 10^{-6}$	
δ_2	——		7.668	

was always higher for pine, regardless of site and year (P < 0.01), except in 2013 at the WAI-0.65 site (Fig. 7). The number of cycles with increment phase was also lower in the 2012 drought year, regardless of species and site (P < 0.01), but with no significant differences for oak at the WAI-0.22 site.

3.4. Weather drivers of the radial increment

The results from the fitted model for daily radial increment (Eq. (1)) are shown in Table 2. Statistically significant weather variables that were included in the final model for spring time were mean air

temperature (Tair; ºC), solar radiation (SR; 10KJ/m²), and accumulated rainfall per daily cycle (P; mm). Two additional variables, water deficit (Wd; mm) and mean vapor pressure deficit (VPD; kPa), were significant when all annual periods were taken into account. Mean air temperature, solar radiation, and the amount of rainfall caused higher radial increments. In the annual analysis, however, was negatively affected by water deficit and high vapor pressure deficit values, which were especially acute during summer time.

Interaction between weather variables and species was not significant, so the species dummy variable only affected the intercept (α_1). The value of this coefficient was negative regardless of the analysis time scale, showing the species growth effect of lower radial increment for oak than pine. Therefore, species responded to identical weather variables in the same way (linearly) but with higher radial increment reaction for pine species.

4. Discussion

4.1. Species-specific stem radial variation cycles by seasons

The dynamics of the stem size cycles might provide valuable information about water status (reversible process) and radial tree growth (irreversible process) (Turcotte et al., 2011; Vieira et al., 2013; Zweifel, 2016). We found differences in radial variation cycles across seasons and species, which support our first hypothesis. Differences observed in amplitude and period features from daily cycles provide insights into the relative changes in transpiration and/or soil water status over time (Deslauriers et al., 2007, 2003; Turcotte et al., 2011).

We observed stem contraction generally from early morning until evening, reflecting the daily cycle of water uptake and loss, as in previous studies (Oberhuber et al., 2015; Vieira et al., 2013). Several authors have found that most diurnal stem shrinkage occurs in the cambial zone, bark, and phloem, and that diurnal variation in the xylem cylinder is relatively small (Drew and Downes, 2009). However, the increase in daily stem diameter variation in spring is partly due to the refilling of the internal stem storage pool, in addition to stem growth (Steppe et al., 2006). Thus, growth and species-specific potential pressure increment in the stem storage compartment could drive spring amplitude differences. Pine is an early successional and light-
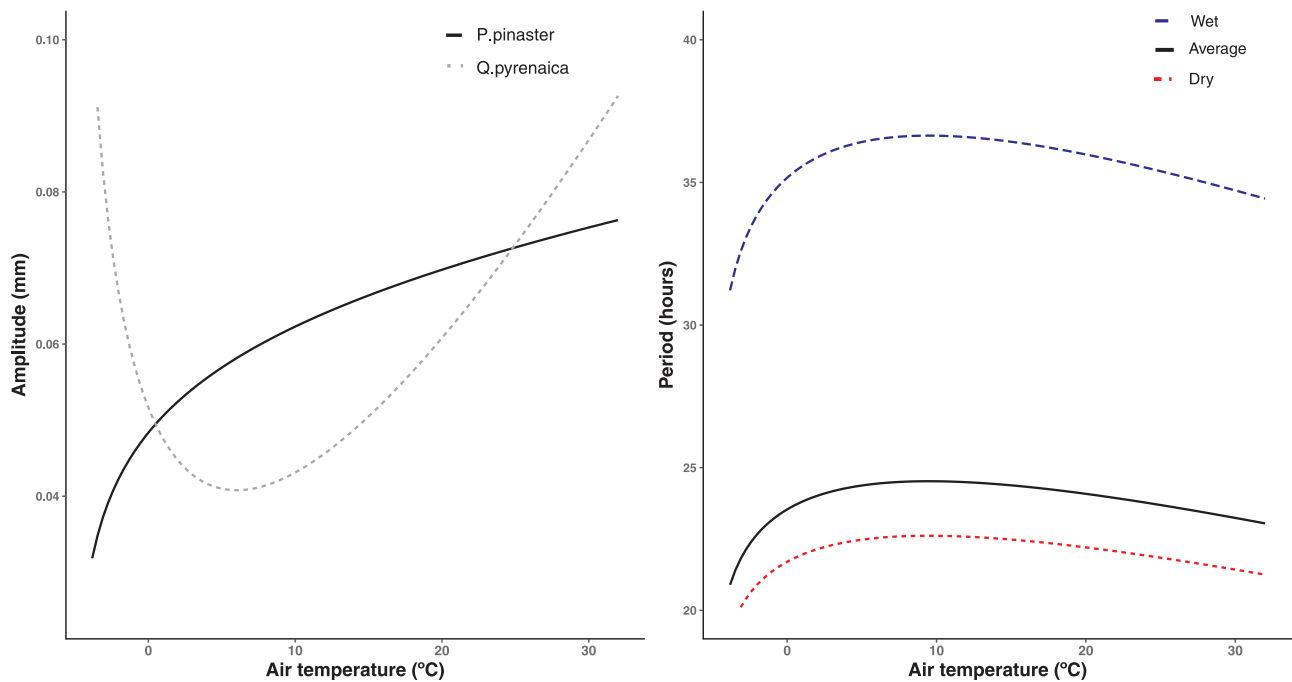
Fig. 6. Species-specific effect of air temperature on amplitude of daily radial variation cycles (left). Air temperature and precipitation effects on period of radial variation cycles for both species (right). Simulation from the fitted linear mixed models for the air temperature and precipitation range. "Wet" weather corresponded to the 95th percentile of daily precipitation range and "Dry" weather corresponded to no rain.
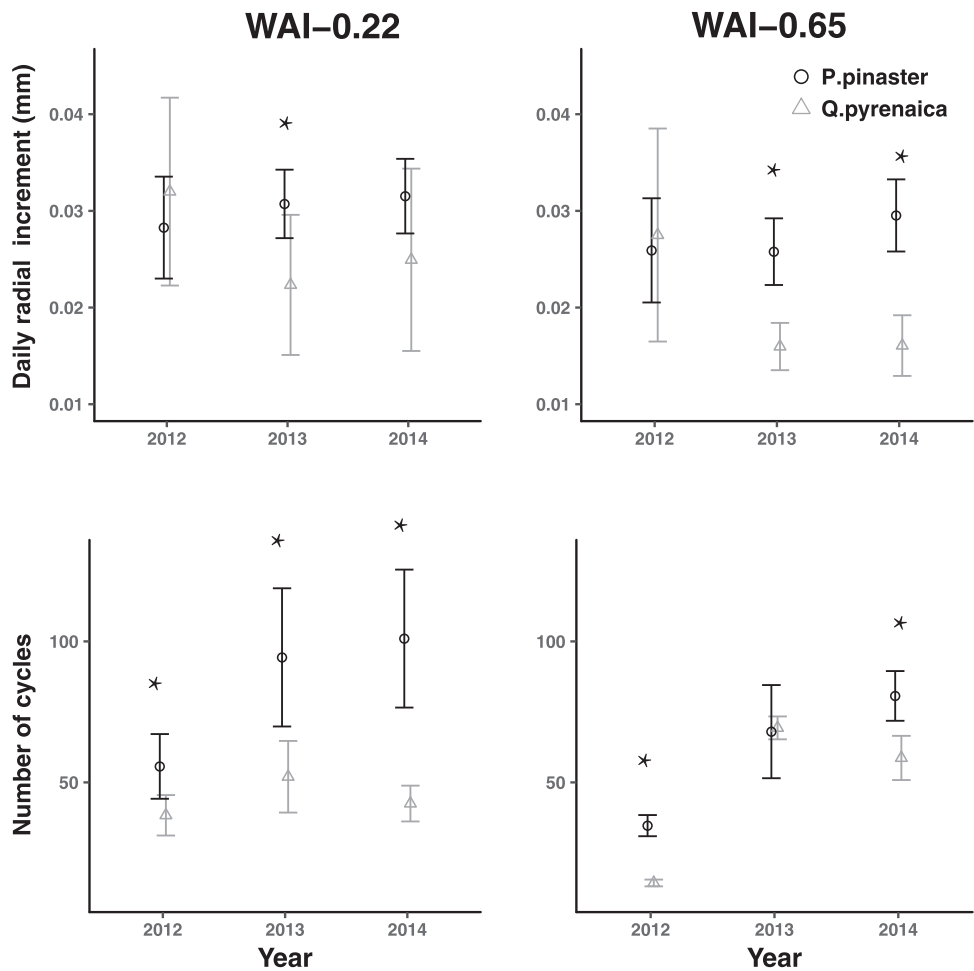

Fig. 7. Differences of daily radial increment and number of cycles with increment phase in spring by site, year, and species. Error bars indicate confidence intervals (95%), asterisk denotes significant differences between species.

Table 2

Model fitted for annual and spring daily radial increment (Eq. 1). Significant parameters are in bold. α_0 and α_1 are the intercept regression coefficients for pine and oak, respectively; T_{air} is air temperature (ºC);SR is solar radiation (10KJ/m2); Wd is water deficit (mm); VPD is mean vapor pressure deficit (kPa); P is daily precipitation(mm); σ_k is standard deviation for year random effect; σ_{jk} is standard deviation for site random effect; σ_{ijk} is standard deviation for tree random effect; σ_e is standard deviation for error term; φ and θ are autoregressive and moving average for annual and spring residual serial correlation parameters from AR(1) and ARMA(1,1), respectively; δ_1 and δ_2 are function parameters used to model residual variance as constant plus a power of the absolute value of the variance covariate (g_{ijk}): $Var(\varepsilon_{ijk}) = \sigma_e^2 (\delta_1 + |g_{ijk}|^{\delta_2})^2$.

Parameter	Annual		Spring	
	Coefficient	p-value	Coefficient	p-value
α_0 (pine)	**$7.38 \cdot 10^{-3}$**	**< 0.001**	**$5.98 \cdot 10^{-3}$**	**0.002**
T_{air}	**$5.15 \cdot 10^{-4}$**	**< 0.001**	**$9.76 \cdot 10^{-4}$**	**< 0.001**
SR	**$4.33 \cdot 10^{-4}$**	**< 0.001**	**$6.38 \cdot 10^{-4}$**	**< 0.001**
Wd	**$-1.68 \cdot 10^{-2}$**	**< 0.001**	n.s.	n.s.
VPD	**$-4.39 \cdot 10^{-3}$**	**< 0.001**	n.s.	n.s.
P	**$2.55 \cdot 10^{-3}$**	**< 0.001**	**$1.68 \cdot 10^{-3}$**	**< 0.001**
α_1 (oak)	**$-2.57 \cdot 10^{-3}$**	**0.002**	**$-8.12 \cdot 10^{-3}$**	**< 0.001**
σ_k (year)	$3.36 \cdot 10^{-7}$		$1.46 \cdot 10^{-3}$	
σ_{jk} (site)	$1.08 \cdot 10^{-3}$		$4.08 \cdot 10^{-8}$	
σ_{ijk} (tree)	$7.88 \cdot 10^{-4}$		$3.17 \cdot 10^{-7}$	
σ_e (error)	1.58		2.18	
φ	0.43		$8.77 \cdot 10^{-1}$	
θ	——		$-6.29 \cdot 10^{-1}$	
δ_1	$2.01 \cdot 10^{-3}$		$1.96 \cdot 10^{-3}$	
δ_2	1.15		1.32	

demanding species, so higher growth is expected during springtime (Aldea et al., 2017; Sánchez-Costa et al., 2015). Our results showed that the greatest amplitude in the daily variation cycle for pine occurred in spring. However in the findings of Vieira et al. (2013), this occurred in pre-summer, similar than oak species in the current study.

Increased transpiration due to high air temperatures leads to elevated demand for water, which is scarce in summer time and provokes extreme contraction from shrinkage (Sánchez-Costa et al., 2015; Vieira et al., 2015; Zweifel, 2016). Accordingly, cumulative annual radial increment patterns confirmed a marked bimodal pattern for both species regardless of the year (Fig. 3) as a consequence of summer drought, which is typical in Mediterranean environments (Albuixech et al., 2012; Camarero et al., 2010). Contrasting climate and stand conditions could explain the differences between our results and those of Vieira et al., (2013) with regard to pine summer daily amplitude patterns (Mediterranean climate with ocean influence and less dense monospecific stand in the latter). Differences in daily cycle amplitude between species during summer time could also be related to distinct canopy transpiration rates and water demand. The higher leaf surface area of oak implies greater diurnal evapotranspiration, which might cause internal stem water reserves to deplete more quickly in oak than in pine. The stem water storage capacity of pine might be higher due to its greater conductivity area in sapwood and bark (Oberhuber et al., 2014), and further accentuated by greater diameter. Generally lower temperatures and photoperiods during autumn induced a decrease in physiological activity, leading to low amplitude and high period in daily radial cycles (Figs. 4 and 5). Although Vieira et al., (2013) showed lower amplitude for pine in autumn, we observed the lowest amplitudes in winter regardless of species, which better corroborates with Biondi and Rossi, (2015). During winter, the circadian cycle of stem size becomes irregular, with marked phase shifts due to temperature. This is the dominant factor in stem size fluctuations in the absence of growth (Biondi and Rossi, 2015) and is attributed to water osmotic movement due to temperature changes near the sap freezing point (Zweifel et al., 2000; Zweifel and Häsler, 2000). However, unlike what commonly occurs at high altitudes and latitudes, the cycles were not inverted at our study sites. This indicates that the sap did not reach the freezing point, as Vieira et al., (2013) also reported in a Mediterranean location.

Furthermore, differences in winter cycle period between species – which are higher for oak than pine (Figs. 4 and 5) – could be due to anatomical differences (sapwood, cell walls, and vessels) that govern water relocation and are directly related to the higher hygroscopicity of oak compared to pine (Popper et al., 2005), i.e., oak might take up water from the environment faster than pine and lose it more slowly, contributing to longer daily cycle periods.

4.2. Meteorological drivers of daily radial variation cycles

We found that temperature drove differences between species in amplitude cycles, whereas the effect of precipitation was similar (Fig. 6 and Table 1). This partially demonstrated our second hypothesis. The relation between air temperature and stem cycle amplitude in our study showed clear increases in amplitude with increased temperature, as found by King et al., (2013). This suggests a higher contraction phase due to the depletion of stem water reserves in response to greater evaporative demand, which is driven by warmer temperatures. Similarly, increased water deficit resulted in a greater amplitude of the radial variation cycle (Table 1), which could also explain the high amplitude during summer time (Figs. 4 and 5). Turcotte et al., (2011) reported that water deficit during the day led to a pronounced contraction phase for boreal black spruce. We also found that rain increased the amplitude cycles (Table 1) and was related to rehydration processes (Deslauriers et al., 2007; Vieira et al., 2013).

The amplitude of radial variation cycles during winter was related to species-specific responses to freezing events (Fig. 6 and Table 1): pine decreased in amplitude, while oak increased at temperatures below approx. 6 °C. This minimum daily amplitude coincides with temperature thresholds for the onset of xylogenesis and general vegetative biological activity (Rossi et al., 2008). Vieira et al., (2013) reported a similar pattern for maritime pine in a Mediterranean area, while King et al., (2013) reported amplitude increment for spruce and larch at freezing temperatures, which resembles the behavior of oak. Extracellular water begins to freeze at low temperatures. This induces osmotic withdrawal of intra-cellular water, causing the cells and eventually the stem to shrink (Pearce, 2001; Strimbeck et al., 2008; Zweifel and Häsler, 2000). Therefore, we hypothesize that daily amplitude divergence at low temperatures may be due to species differences in the sap freezing point. An alternative and perhaps simpler hypothesis relates to differences in bark width, which might serve as thermal insulation. We also observed (results not shown) sudden large decreases in stem size for pine species at low temperatures, based on the same physiological process. However, winter temperatures below 0 °C are very rare at both sites, which made it impossible to find a significant statistical relationship indicating increased amplitude at lower temperatures for pine species.

Moreover, higher amplitude for pine in a large temperature range might be related to higher radial increment rates, especially in spring (Fig. 3 and Table 2). Daily amplitude differences between species at high temperatures (above 25 °C), could be related to evapotranspiration and water availability, which lead to distinct stem shrinkage responses. However, species did not show a different response to weather variables for the duration of full daily radial cycle (Table 1). Thus, only weather variables (temperature and rain) controlled the period of radial variation cycles, as reported by Vieira et al., (2013). Here, we found that period decreased with increased temperature. Thus, when temperatures are especially high and the days are longer during pre-summer and summer, transpiration rates may be also high, causing faster contraction and higher recovery duration (results not shown), resulting in a compressed wave period (Figs. 4 and 5). Deslauriers et al. (2007) demonstrated that vapor water deficit had a direct effect on the duration and amplitude of the contraction phase, which may corroborate our results.

Additionally, the fitted model (Table 1) indicated that the period of radial variation cycles decreased at air temperatures below 8.5 °C. We

suggest that temperatures close to freezing may generate a faster contraction phase due to thermal response, leading to radial variation cycles with a compressed period. Although air temperature certainly plays a role in the radial variation cycle period, precipitation is more closely linked to higher period duration because of rehydration (Fig. 6).

4.3. Meteorological drivers of radial increment phase

We expected species-specific responses to weather in radial increment phase based on light demand, root system or leaf phenology features differences. However, the two species responded to the same weather variables and in the similar way (linearly) modifying radial increment. Accordingly, trees generally revealed a synchronous shrinking and swelling cycle response at the site level (data not shown) corresponding to daytime, when trees transpire quickly, and nighttime, when processes leading to water depletion or replenishment occur rapidly. This finding agrees with that of Sánchez-Costa et al., (2015) who reported coordinated responses of transpiration, water storage dynamics, and growth-based water use efficiency in Mediterranean pine and oak species. These evidences could suggest a strong functional convergence between co-existing species, resulting in competition for resources at least in some periods. Conversely, in a previous study we found species-specific intra-annual radial increment responses to weather variables. Although precipitation, solar radiation and vapor pressure deficit influenced both species, radial increment in oak trees also showed sensitivity to minimum temperature and relative air humidity (Aldea et al., 2017). This may be explained by methodological and precision differences in estimating radial increment (biweekly rate vs. daily cycle analysis).

Overall, pine responded to weather with higher radial increment compared to oak (Table 2), which again supports partial acceptance of the second hypothesis. These differences are also shown in Fig. 7 according to the year and site. In years with low spring precipitation, such as 2012 and 2014 at WAI-0.22 and 2012 at WAI-0.65 (Fig. 1), the difference between species seems to disappear. However, the number of daily cycles with increment phase was always higher for pine (Fig. 7), except in 2013 at WAI-0.65, indicating a probable species-specific growth strategy (evergreen vs. deciduous). We hypothesized that pioneer species are greater resource expenders and develop riskier life strategies for capturing resources, so radial increment onset would occur earlier for pine. In contrast, shade-tolerant species such as oak utilize resources more efficiently and may develop safer life strategies (Cuny et al., 2012). Leaf budburst and foliation differences may allow pine to take advantage of soil water reserves, because oak is still leafless in early spring and lives on the reserves of the previous year (Fernández-De-Uña et al., 2017). As a pioneer species, deeper rooting and higher light demand may give pine a competitive advantage. However, lower daily radial increment of oak trees may be related to differences in reproduction methods (seed vs. coppice) or tree competition (higher for oak trees)(Linares et al., 2009; Rathgeber et al., 2011; Vieira et al., 2015).

The third hypothesis was confirmed: temperature, precipitation, and water deficit had an important role in driving radial increment, though solar radiation and vapor pressure deficit also affected it. Several authors have found positive correlations between air temperature and radial increment (Deslauriers et al., 2003; King et al., 2013; Van der Maaten et al., 2013), though other works report the opposite due to elevated transpiration rates, especially in summer (Deslauriers et al., 2007; Oberhuber et al., 2014).

Our results corroborated that precipitation is an important factor in radial increment in Mediterranean areas, as it allows growth and/or replenishment of internal water reserves in trees. We observed a low precipitation in autumn 2011 and spring 2012 which provoked an extreme drought in 2012 at both locations, resulting in low cumulative radial increment for both species (Fig. 3). However, high winter or spring rainfall during 2013 and 2014 increased annual cumulative radial increment, despite summer drought. Precipitation events increase available soil water, which is essential for photosynthesis and growth, but there is also evidence that rain plays a role in the stem rehydration process. The difficulty in differentiating these two effects with dendrometers leads to overestimation of the role of rain (Biondi and Rossi, 2015; Turcotte et al., 2011; Zweifel, 2016).

At the tree physiological level, the negative effect of high vapor pressure deficit concurs with other studies (Aldea et al., 2017; Oberhuber et al., 2014; Van der Maaten et al., 2013) and can be explained by increased evapotranspiration, which inhibits cell enlargement and growth (Oberhuber et al., 2014). Water deficit is also related to climate variables which influence transpiration (Oberhuber et al., 2015). This suggests that drought from June to August is a highly prominent factor in limiting growth for both species, as we observed for 2012. Though solar radiation promotes radial increment and could be related to photosynthesis and eventual growth, these relationships weaken or are modified in a situation of water deficit (Muller et al., 2011), implying subsequent increases in transpiration rates, closed stomata and stem contraction (Duchesne and Houle, 2011).

5. Conclusions

The results of our study provided insight into environmental control of intra-annual radial increment in co-occurring species exposed to drought. The same weather variables drove radial increment for both species, though pine response was greater.

Air temperature and rain altered the amplitude and period for daily stem radial variation cycles, while water availability (rain vs. water deficit) seemed to be crucial for the radial increment phase. Therefore, increased temperatures and higher frequency of drought events, which are forecasted for the Mediterranean region based on climate change scenarios, may alter radial variation cycles and cause a similar reduction in radial growth for both species. However, due to radial increment differs between species, we theorize that under drought conditions oak trees would reach radial growth stagnation earlier, endangering the stand stability. This became evident in 2012 due to a severe drought at both study sites. Competition control via thinning treatment could improve resource availability and modify tree dominance. This in turn would affect cambial activity, promoting earlier start, higher growth rates and longer growing seasons (Aldea et al., 2017; Rathgeber et al., 2011; Vieira et al., 2015). For oak trees especially, a forest management strategy focused on enhancing radial growth may be necessary to offset ecological changes affecting species survival and the decreased production that could accompany climate change predictions.

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